

Some Aspects of the Ecology of *Ophioglossum engelmannii* in the Cedar Glades of Kentucky and Tennessee

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Ophioglossum engelmannii Prantl (Ophioglossaceae) is a North American fern whose reported geographical range extends from Florida to Arizona and south-central Mexico north to northwestern Virginia, southern Ohio, southern Indiana, Missouri, Kansas, and Oklahoma. Plants of this species have been found growing in prairies, in open, grassy woodlands, on bluffs, in clay barrens, and in cedar (limestone) barrens and glades (Clausen, 1938; Fernald, 1950). Throughout its range, *O. engelmannii* is restricted to limestone soils, and thus Palmer (1932) considered it a strict calciphile. In a study of its soil reaction preferences, Wherry (1926) found that *O. engelmannii* is restricted to soils with a neutral to slightly alkaline pH. Information on macro-geographical distribution and general habitats of the species, as well as taxonomic data, can be found in several taxonomic works (Clausen, 1938; Fernald, 1950; Shaver, 1954; Gleason, 1952). The anatomy of the vegetative organs, as well as some aspects of sexual reproduction, also have been studied (Bold, 1967). Although this unusual fern is of much interest to botanists, little information is available on its autecology. Thus, the purpose of this paper is to report (1) observations made on the ecology of *O. engelmannii* in cedar glades of Kentucky and Tennessee, with special reference to its vegetative life cycle and (2) results of laboratory studies on the temperature relations of bud growth and dormancy.

DISTRIBUTION, HABITAT, AND PLANT ASSOCIATES

In Kentucky *O. engelmannii* has been reported from Barren, Boone, Calloway, Clark, Edmonson, Logan, Marshall, Rockcastle, Simpson, Warren, and Wayne Counties (Braun, 1936; Reed, 1958; McCoy, 1938; McCoy & Hunter, 1968), and we have found it in Bullitt County, making a total of 12 counties in which the species is known to occur. Shaver's (1954) map of its distribution in Tennessee shows that the species occurs in Bedford, Davidson, Decatur, Franklin, Knox, Marion, Marshall, Maury, Montgomery, Rutherford, Smith, Williamson, and Wilson Counties. Specimens from Hamilton and Meigs Counties are in the University of Tennessee herbarium (A. M. Evans, pers. comm.). In addition, we have found it growing in Sumner and Giles Counties, making a total of 17 counties in Tennessee (Fig. 1).

In both states the populations of *O. engelmannii* are restricted to areas with shallow, limestone soils (cedar glades or cedar barrens). Some populations occur on relatively large, well-developed cedar glades (e.g., those in Bullitt and Simpson Counties, Kentucky and Marshall, Rutherford, and Wilson Counties, Tennessee), where *O. engelmannii* grows in association with a number of characteristic herbaceous cedar glade species. However, other populations occur on small rock

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Volume 64, number 2, of the JOURNAL was issued June 28, 1974.

outcrops, where *O. engelmannii* may be associated with only one or two characteristic cedar glade species.

Within the cedar glades, plants of *O. engelmannii* usually are found growing on the open glades (i.e., areas where the soil is too shallow to support shrubs or trees), although occasionally they grow at the edges near deciduous shrubs. Soil depths in open glades range from 0 to 25 cm and occasionally up to 50 cm in deep, soil-filled cracks. Plants of *O. engelmannii* generally are restricted to soil that is 5–15 cm deep, but they are most abundant in soil that is 10–15 cm deep. In glades developed on thin-bedded limestone, soil has accumulated among rock fragments and in crevices; in glades developed on thick-bedded limestone, a layer of soil has formed over a massive bed of limestone. In both types of glades the soil is saturated with water during late autumn, winter, and early spring, but during late spring, summer, and early autumn it is subject to long periods of drought.

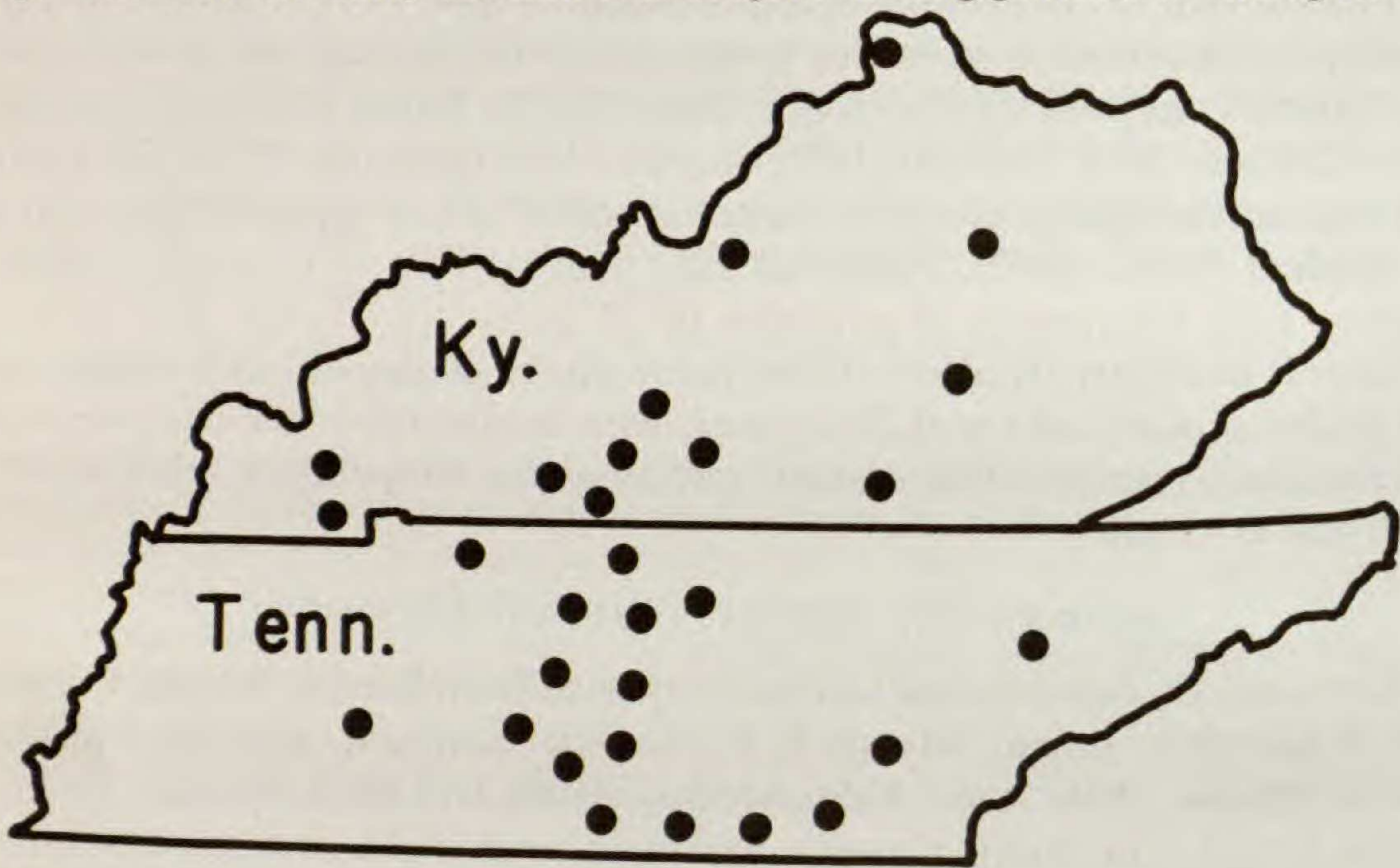


FIG. 1. Geographical distribution of *O. engelmannii* in Kentucky and Tennessee.

The most common and abundant associate of *O. engelmannii* in the cedar glades of Kentucky and Tennessee is the summer annual, xerophytic grass *Sporobolus vaginiflorus*. This grass is the dominant species in much of the open glade community (Baskin & Baskin, 1973). Other common associates in the cedar glades include *Ruellia humilis*, *Scutellaria parvula*, *Nothoscordum bivalve*, *Heliotropium tenellum*, *Agave virginica*, *Petalostemon gattingeri* (in central Tennessee), and *Diodia teres* (in Bullitt County, Kentucky).

In the Ozark Region of Arkansas and Missouri *O. engelmannii* grows on limestone ledges or glades in shallow soil that is saturated with water in spring but which later becomes quite dry. The species also occurs on clay and gravel banks, but always in calcareous soil (Palmer, 1932). In a shallow-soil habitat on Mississippian limestone in Missouri, Palmer (1914) lists the following species as associates of *O. englemannii*: *Bouteloua curtipendula*, *Allionia albida*, *Tragia ramosa*, *Malvastrum angustum*, *Sedum pulchellum*, and *Opuntia* sp. Elsewhere,

O. engelmannii has been found growing in prairie-like situations and in association with prairie species. Braun (1927) described this kind of habitat in Ohio and listed the following associates: *Andropogon scoparius*, *Bouteloua curtipendula*, *Agave virginica*, *Lithospermum canescens*, *Senecio balsamitae* and *Blephilia ciliata*.

PHENOLOGY

Phenological observations were made on *O. engelmannii* in the middle Tennessee cedar glades from April 1969 to September 1973 and in the Kentucky glades from March 1972 to September 1973. Some observations were made on populations in four counties in Kentucky and eight in Tennessee, but the most detailed observations were made on populations growing in Bullitt and Simpson Counties, Kentucky and in Rutherford and Wilson Counties, Tennessee. Most of the observations on bud growth were made in a glade in Bullitt County, Kentucky that had been surveyed for development and was later destroyed.

Plants of *O. engelmannii* have a short, vertical rhizome about 0.5 cm long, the top of which is 1–2 cm below the soil surface. This rhizome is attached to the upper side of a large, straight, horizontal root that often extends 5 to 10 cm on both sides of the rhizome. According to Bold (1967) and Shaver (1954), this basal root produces adventitious buds which develop into new plants, resulting in the production of large colonies of asexually produced plants. We have observed this many times in the field. From the sides of the erect rhizome arise 5–15 unbranched roots that, for the most part, grow horizontally. Leaf buds are produced at the rhizome apex. A complete leaf consists of a sterile leaflet (blade) and a stalked, spike-like fertile leaflet (fertile spike). A single plant can produce one or two leaves at a time, and the leaf (or leaves) may or may not be fertile. The leaves turn green long before they reach the soil surface, indicating that light is not required to produce chlorophyll.

To determine the number of plants that produce (1) one leaf, (2) one leaf and one fertile spike, (3) two leaves, and (4) two leaves and two fertile spikes, a total of eleven 1-meter square quadrats were established in four cedar glades in Tennessee and Kentucky, and all the plants in each of them were examined for number of leaves and fertile spikes (Table 1). A total of 2,869 plants were present in the 11 quadrats, and of these 2,367 (82.5%) had one leaf and 502 (17.5%) had two leaves. The smallest number of plants per quadrat with two leaves was 19 (7.5%) and the largest was 101 (44.7%). Only 292 (10.2%) of the 2,869 plants had fertile spikes and only 43 (1.5%) of the plants had two fertile spikes. No plants with one fertile and one sterile leaf on the same rhizome were present in the quadrats. However, in May 1974 we saw a few plants with one fertile and one sterile leaf in Simpson County, Kentucky and in Rutherford County, Tennessee.

Leaves begin to emerge from the soil in mid March, and by mid April they are fully expanded. In plants that produced a fertile spike, it is inside the rolled blade as it emerges from the soil. The spike does not elongate as fast as the leaf, and thus does not reach its full length until late April. Sporangia begin releasing spores during the first week of May, and by the first week in June all of them have been released. During drier years or in drier microhabitats all of the spores may be

released within two weeks. The leaves begin to turn yellow in mid-May, and by late May and early June, depending on habitat moisture, the plants are dormant.

All plants in a population produce leaves in the spring, but in late summer and autumn only a few leaves emerge, and only a few of these are fertile. The number of leaves that emerges appears to be related to soil moisture. In years with wetter summers and autumns or in wetter habitats in the same year, more leaves emerge than in drier years or in drier habitats. The leaves that emerge during summer and autumn are killed before winter, and the plants are dormant during the winter. Leaves that emerge during wet periods in August may be killed during late summer or early autumn by drought; or if soil moisture permits, they may remain green until killed by low temperatures in late autumn. Those that emerge in early autumn generally are killed by low temperatures in late autumn, rather than by drought.

TABLE 1. NUMBER OF LEAVES AND FERTILE SPIKES ON PLANTS OF *O. ENGELMANNII*.

Location & date	Quad. No.	Total No. Pls.	1 leaf & no spike		1 leaf & 1 spike		2 leaves & no spike		2 leaves & 2 spikes	
			No.	%	No.	%	No.	%	No.	%
Bullitt County, Ky. 6 May 1973	1	236	158	66.9	22	9.3	51	21.6	5	2.1
	2	436	379	86.9	22	5.0	35	8.0	0	0.0
	3	444	387	87.2	16	3.6	37	8.3	4	0.9
	4	127	84	66.1	3	2.4	39	30.7	1	0.7
	5	235	189	80.4	5	2.1	41	17.4	0	0.0
Simpson County, Ky. 15 May 1973	1	253	204	80.6	30	11.9	19	7.5	0	0.0
	2	383	276	72.1	71	18.5	31	8.1	5	1.3
Rutherford County, Tenn. 15 May 1973	1	146	71	48.6	25	17.1	46	31.5	4	2.7
	2	291	237	81.4	21	7.2	30	10.3	3	1.0
Wilson County, Tenn. 16 May 1973	1	92	55	59.8	7	7.6	29	31.5	1	1.0
	2	226	78	34.5	27	11.9	101	44.7	20	8.8
Totals	11	2,869	2,118	73.8	249	8.7	459	16.0	43	1.5

Autumn emergence of leaves and fertile spikes of *O. engelmannii* has been reported in the Ozark Region of Missouri and Arkansas (Palmer, 1932), near Norman, Oklahoma (Couch, 1937), and in eastern Kansas (Magrath & Weedon, 1972). Palmer (1932) and Couch (1937) indicated that autumn growth was associated with periods of high soil moisture, just as it is in the cedar glades of Kentucky and Tennessee.

By the time a leaf is fully expanded, in either spring or autumn, a new leaf bud is present on the rhizome at the base of the petiole of the expanded leaf. To follow the growth of shoot buds produced in spring, 80 plants were removed from the Bullitt County population at irregular intervals from June 1972 until February 1973. The length of each bud was measured to the nearest millimeter; lengths of buds collected on various dates are given in Table 2. The buds that were measured in November, January, and February are buds that were initiated the previous spring. Because the autumn of 1972 was dry, very few plants in the population had leaves to emerge; therefore, new buds were not produced. Although bud

growth was slow, some did occur during summer, autumn, and winter; there was no period of rapid extension. The tips of buds collected on 25 February 1973 had almost reached the soil surface. By 19 March the leaves had emerged and were 2–4 cm above the soil surface.

TEMPERATURE RELATIONS OF BUD DORMANCY AND GROWTH

Phenological events in the vegetative life cycle of *O. engelmannii* are related directly to bud growth and dormancy. In order to understand the vegetative life cycle of this species, external and internal factors controlling bud growth and dormancy should be identified.

In the cedar glade habitat, soil moisture is not a limiting factor in the growth of *O. engelmannii* from mid-autumn to mid-spring; it may or may not act as a limiting factor from mid-spring to mid-autumn. Obviously, if the habitat is very dry, soil moisture will limit growth, even if buds are physiologically non-dormant and other external factors are optimum for growth.

TABLE 2. GROWTH OF BUDS OF *O. ENGELMANNII* IN CEDAR GLADES.

Collection date	Mean length \pm SE (mm)
5 June 1972	3.3 \pm 0.2
3 July 1972	3.5 \pm 0.3
7 Aug. 1972	5.2 \pm 0.3
24 Nov. 1972	8.9 \pm 0.3
21 Jan. 1973	10.3 \pm 0.4
25 Feb. 1973	11.1 \pm 0.4

Under non-limiting soil moisture conditions, temperature and light are the two most important external factors controlling vegetative growth of plants in their natural habitats. Since the buds of *O. engelmannii* are below ground and are physiologically non-dormant when they emerge above ground, light can be ruled out as a factor that breaks dormancy or initiates growth in this species. Thus, it would appear that temperature controls bud dormancy and growth and the seasonal vegetative life cycle of this species.

This study was restricted to temperature relations of bud dormancy and growth of buds formed in spring. All plants used in the experiments were collected from the cedar glade in Bullitt County, Kentucky that since has been destroyed. As mentioned above, it was very dry in this glade during autumn of 1972. As a result, very few of the plants produced summer buds; almost all of the buds in the population were spring-formed.

The purpose of the first experiment was to determine if buds are innately dormant when the spring-formed leaves die in late spring or if they remain quiescent due to temperatures and/or soil moisture conditions that are unfavorable for leaf emergence. On 5 June 1972, 160 plants were collected from the glade and each plant was placed on a 5 cm layer of moist sand in a styrofoam cup with drainage holes in the bottom. The plants were only partially covered with sand so that the buds could be examined and measured to the nearest millimeter without disturbing the plants. Twenty plants were placed in each of eight enamel trays, and then the trays were wrapped with aluminum foil to provide darkness. A tray containing

20 plants was placed at each of four constant temperatures (10, 15, 20, and 25° C) and four alternating temperatures (15/6, 20/10, 30/15, and 35/20° C) in temperature-controlled incubators. The alternating temperature regimes (12/12 hr thermoperiods) were selected to represent the mean daily maximum and minimum monthly temperatures that might occur in the *O. engelmannii* habitat during the growing season. The temperatures used and the month(s) to which these correspond are: March 15/6° C, April 20/10° C, May 30/15° C, June 30/15° C, July 35/20° C, August 35/20° C, September 30/15° C, October 20/10° C, and November 15/6° C. These temperatures closely approximate soil temperatures 2.5 cm below bare ground on a flat surface in Lexington, Kentucky for the respective months given (Jerry Hill, pers. comm.). Bud length on each plant was measured to the nearest millimeter at 5-day intervals in a darkened room with the aid of a green safe light, and the sand was watered, if needed, while the plants were exposed to the green light.

TABLE 3. GROWTH OF NEWLY INITIATED BUDS OF *O. ENGELMANNII* AT CONSTANT AND ALTERNATING TEMPERATURES IN THE LABORATORY.

Temp. (°C)	Mean length \pm SE initial	Mean length \pm SE after 30 days	Difference
10	3.7 \pm 0.5 mm	3.9 \pm 0.6 mm	0.2 mm
15	2.8 \pm 0.3	3.3 \pm 0.2	0.5
20	2.8 \pm 0.3	3.1 \pm 0.2	0.3
25	3.6 \pm 0.5	4.1 \pm 0.5	0.5
15/6	2.7 \pm 0.3	2.7 \pm 0.3	0.0
20/10	3.1 \pm 0.2	3.8 \pm 0.5	0.7
30/15	3.9 \pm 0.6	5.0 \pm 0.8	1.1
35/20	3.2 \pm 0.4	3.8 \pm 0.4	0.6

In late spring and early summer, buds of *O. engelmannii* are innately dormant (Table 3). That is, the lack of leaf emergence is due to some physiological factor(s) within the bud and not to environmental conditions. Although some growth (1.1 mm or less) occurred at all temperatures tested except 15/6° C, it was not nearly enough to bring the leaf above the soil surface. A bud would have to grow 1–2 cm before the tip of the leaf would be above the soil surface.

To study the influence of temperature on shoot emergence in freshly dormant plants, 20 plants collected on 5 June 1972 were placed at each of the four constant and four alternating temperatures. Each plant was planted in greenhouse potting soil in a styrofoam cup, and the top of the rhizome was 2 cm below the soil surface. The soil in each cup was kept moist, and the cups were checked for emergent leaves at 10-day intervals from 5 June until 12 November 1972. A leaf was considered to have emerged when its tip was 0.5 cm above the soil surface.

Leaves of some of the plants at 35/20, 30/15, 20/10, and 25° C emerged (Fig. 2). Leaf emergence was greatest at 35/20 and 30/15° C, where 18 and 16 leaves, respectively, came above the soil. For the most part emergence began in late July and continued into early October. On 12 November, ten of the plants at 10, 15, 15/6, and 20/10° C that had not produced an emergent leaf were placed at 30/15° C for 30 days. About half of the plants at 30/15° C produced leaves (3, 4, 6, and 6 of the plants removed from 10, 15, 15/6, and 20/10° C, respectively); whereas, only three of those left at the original temperatures produced leaves (2 at 10° C and 1 at

15° C). Thus, it appears that although high temperatures are not absolutely necessary to overcome dormancy, buds lose their dormancy much faster at high than at low temperatures. Also, high temperatures are required for growth after the buds are no longer dormant.

To obtain information on the influence of winter field conditions on rate of shoot emergence and the temperatures required for shoot emergence, 80 plants were collected in the field on 21 January and 25 February 1973, and 20 plants were placed at each of the four alternating temperature regimes. Plants were potted in soil with the buds covered to a depth of 2 cm. The soil was kept moist throughout the experiment. The cups were checked for emergent leaves at 5-day intervals for about 2 months.

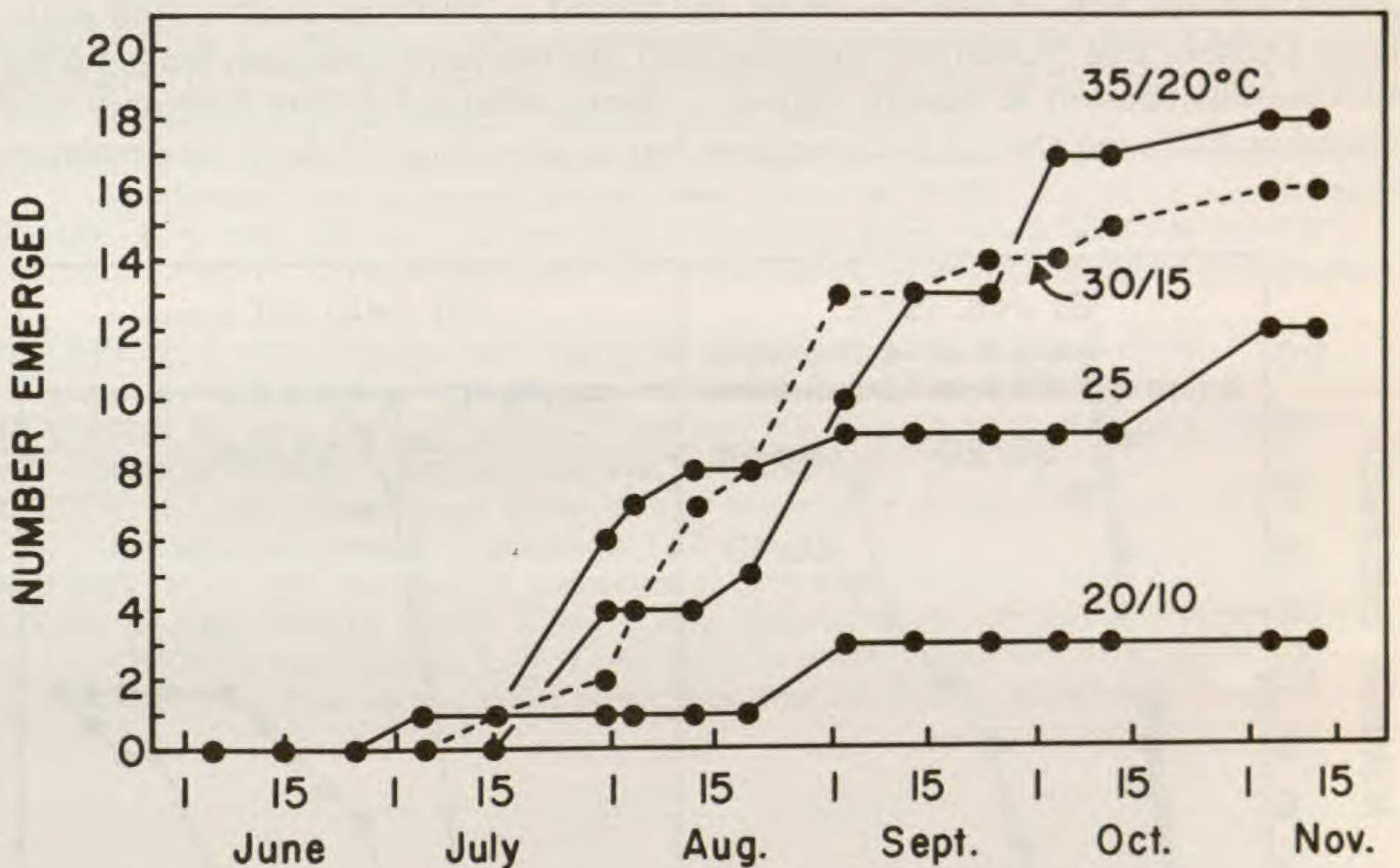


FIG. 2. Effect of temperature on leaf emergence of *O. engelmannii*. Freshly-dormant plants were planted in soil on 5 June 1972. There was no emergence at 10, 15, 20, and 15/6°C.

At 30/15 and 35/20° C essentially all of the leaves of plants from both collection dates emerged after 15 days (Fig. 3). Emergence at 20/10 and 15/6° C, however, was much slower, and, except for plants collected in January and placed at 20/10° C, the number of leaves that came up was reduced by 50% or more. At 20/10° C, 17 of the January-collected plants produced leaves; whereas, only 10 of the February-collected plants did so. At 15/6° C there was a marked increase in rate as well as number of leaves that emerged in the February-collected plants as compared to the January-collected plants. Thus, it appears that although rate of leaf emergence is slow, leaves will grow at low temperatures (15/6° C) after they have overwintered in the field.

DISCUSSION

Freshly dormant buds of *O. engelmannii* are innately dormant, as indicated by their small amount of growth over a wide range of constant and alternating temperatures (Table 3). However, after a short period of dormancy in the field, buds gain the ability to grow slowly at high temperatures (Table 2), and if soil moisture conditions permit, some of the plants produce emergent leaves in late summer and early autumn. Thus, soil moisture in the habitat during this period appears to be a major factor determining shoot emergence. On the other hand, leaf emergence is prevented in late autumn when the soil is moist because temperatures are below those required for growth. Apparently, during the low temperature winter period changes occur in the physiological state of the plants that render them capable of growing at lower temperatures than non cold-treated plants. Whereas plants collected from the field in late November and placed at 20/10 and 15/6° C (the simulated October and November temperatures) did not have emergent leaves after two months (Baskin & Baskin, unpub.), plants collected in late February and placed at 20/10 and 15/6° C had emergent leaves after 9 and 33 days, respectively (Fig. 3).

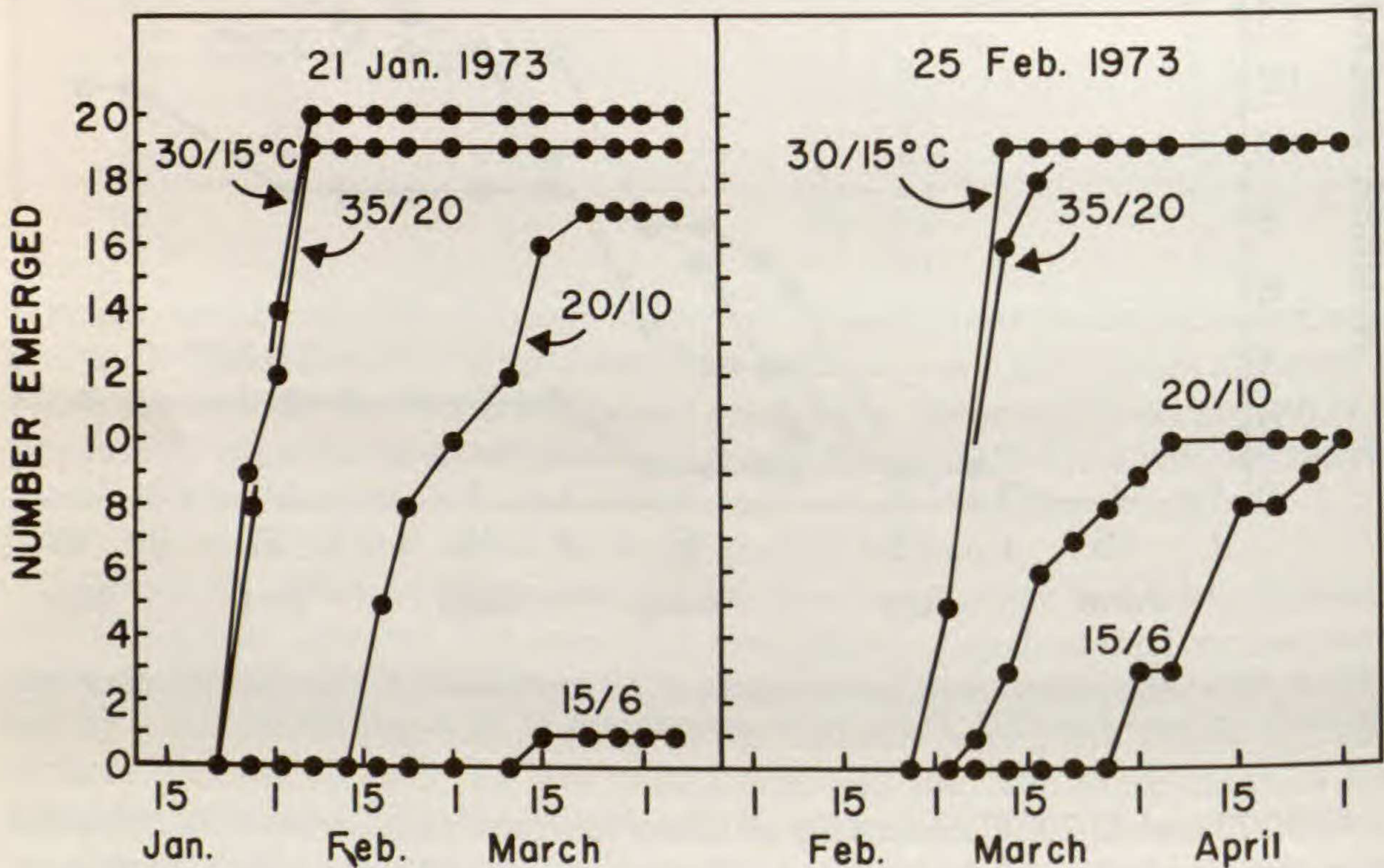


FIG. 3. Leaf emergence of *O. engelmannii* plants at four alternating temperatures. Plants were collected in the field on 21 January and 25 February 1973.

Following the models proposed by Vegis (1963, 1964) for breaking of dormancy in seeds and buds of plants, the emergence of *O. engelmannii* buds from dormancy can be summarized as follows. Newly formed buds are innately dormant when leaves that emerged in spring die in late spring and early summer. From this state of innate dormancy, the buds pass into a state of conditional dormancy when

they will emerge only at high temperatures and at a relatively slow rate. Finally, after a winter period of low temperatures, the buds become completely non-dormant and thus are capable of growing and emerging at a fast rate over a wide range of temperatures.

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